A REVISION OF THE JURASSIC STROMATOPOROIDS *ACTINOSTROMINA*, *ASTROSTYLOPSIS*, AND *TRUPETOSTROMARIA* GERMOVŠEK

by R. G. S. HUDSON

Abstract. Seven species of stromatoporoids described by Germovšek in 1954 from the Tithonian of Jugoslavia are redescribed and allocated to his genera *Actinostromina* and *Astrostylopsis* and placed in the family Actinostromariidae and the superfamily Actinostromariicae *nov*. The genus *Trupetostromaria* Germovšek is considered to be a junior synonym of *Astrostylopsis*. Structural changes illustrated are the development of tubular coenotubes and cellular sclerenchyme, the reduction of the transverse lamellae, and the replacement of normal astrosystems by individual axial astrotubes with the omission, or considerable reduction, of transverse astrotubes, coenosteal structure thus becoming generally tubular.

INTRODUCTION

In 1954 G. Germovšek described various hydrozoans from the Upper Jurassic of Jugoslavia and in doing so founded ten new species of Stromatoporoidea, species not easy to evaluate since some of the technical terms used are of uncertain connotation and many of the illustrations inadequate. Some of the species are allocated to Palaeozoic genera, others to new genera, two of which are grouped to form a new family. It is evident that the species so founded are of importance in any systematic study of the Mesozoic Stromatoporoidea and certain of them have therefore been restudied and are redescribed in this paper. The material described by Germovšek is now in the collections of the Institute of Geology of the Slovene Academy of Science and Arts at Ljubljana and, by the kindness and courtesy of Dr. I. Rakovec, the holotypes and figured thin sections of *Actinostroma grossum grossum*, *A. g. robustissimum*, *Actinostromaria tubulata*, *Actinostromina oppidana*, *Astrostylopsis slovenica*, *A. grabenensis*, and *Trupetostromaria circoporea*, all species founded by Germovšek, have been lent to the author for study. The work resulting in this paper was carried out in the Geological Department of the Iraq Petroleum Company and the author here records his thanks to the Directors and Chief Geologist of that company for those facilities.

All specimens described and figured in this paper are from the Upper Jurassic (Tithonian) of Graben, near Novo mestro, Slovenia, Yugoslavia. The thin sections have been remounted and thus do not exactly correspond to those photographed by Germovšek. Structural dimensions stated in this paper give neither the average nor the range. They are the general dimensions, rather arbitrarily chosen. Measurements across coenotubes, &c., are from one calcification band to the other.

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SKELETAL MORPHOLOGY

Skeletal tissue. Though the microstructure of the various skeletal elements is not as yet understood, it has been recognized that there are at least two fundamental methods of tissue (sclerenchyme) growth of both pillars and lamellae. In one, the crystal fibres which make up most of the sclerenchyme are grouped in fascicles arising from individual centres of calcification, which usually show as clear minute spheres, or from linear centres of calcification showing as vertical clear cylindrical rods. A single succession of such centres would result in a continuing series of fibre fascicles and would form a simple trabecula. Such single series are not known: all recorded sclerenchymal microstructure shows that the crystal fibres arise from groups of solitary or linear centres; all trabeculae are thus compound and individual fascicles can rarely be recognized. These centres are enveloped in fine dark granular tissue or may themselves be darker than the surrounding tissue. Continuing upward repetition, they form in a pillar a dark-coloured calcification strand, and in a lamella a midplane calcification band. Such fibrous secretion is therefore puntal with all fibres directed generally upwards (*clinogonal*). When centres are loosely grouped, the fibres may vary slightly in direction.

In the other (*orthogonal*) method of skeletal secretion, the crystal fibres also originate from a calcification strand, or band, of dark mottled granular calcite in which individual centres cannot be definitely recognized. These fibres are at right angles to the calcification strand (or band) and do not form fascicles. Such fibre secretion is therefore planar or linear and not puntal. In both methods of fibre secretion, the calcification bands may vary greatly in thickness (in some forms they may almost complete the trabeculae, the fibrous envelope being thin).

Much of the distinction envisaged by Germovšek for his various species and genera was based on differences in microstructure of the sclerenchyme. The microstructure of *Actinostroma grossum* and its subspecies was stated to be radially (orthogonal) fibrous; that of *Actinostromaria tubulata* to be between radial and clinogonal fibrous as considered by him to be characteristic of *Epistromatopora*; that of *Actinostromina oppidana* to be finely granular and homogeneous; that of *Astrostylopsis slovenica* to be crystal-fibrous; that of *A. grabenensis* to be granular with no true crystal-fibres; that of *Trupetostromaria circoporea* to be crystal-fibrous in all directions. The author, contrary to Germovšek, considers that they are *all* definitely orthogonal, the main difference between them being in the width of the calcification band and the fineness of the crystal-fibres. The skeletal microstructure of each of the species is figured on Pl. 6.

Coenospaces and coenotubes. The pattern of the reticulum is often a matter of specific importance in the Mesozoic Stromatoporoidea. It is often best expressed not in terms of the shape and direction of its skeletal elements but rather in the form and direction of the spaces between them. To facilitate description a space between pillars or vertical lamellae, or between transverse lamellae, is here called respectively a *vertical* or *transverse coenospace*. When the vertical lamellae are all linked together and form, in transverse section, a net of polygonal or circular mesh, the spaces may be termed *coenotubes*. These often have no great vertical extent.

Fenestrate vertical lamellae. The linking of adjacent vertical pillars by connecting lamellae is effected, both in the Milleporellicae and the Actinostromariicae, by vertical repetition

of transverse trabeculae. The process is not continuous for at regular intervals the trabeculae are not constructed so that any connecting lamella consists of a vertical alternation of vertically joined transverse trabeculae and small gaps, or, possibly, an alternation of single transverse trabeculae and gaps. Connecting lamellae are therefore fenestrate.

Cellular sclerenchyme. Trabecular growth in the vertical lamellae, though generally retaining its vertical and transverse directions, may become irregular and incomplete with the result that the lamellae, instead of being regularly fenestrate, become cellular, the cellules being generally small, rounded, completely enclosed, and completely filled with fibrous tissue. Such lamellae may widen considerably and become, within the reticulum, individual structures of cellular sclerenchyme. In general they retain their vertically lamellate character and act as walls dividing astrosystems, or enclosing astrotubes. Such sclerenchyme is well developed in most of Germovšek's species. It is not unusual in other genera of the Actinostromariicae.

Tubular reticulum. The species founded by Germovšek all have, within the reticulum, solitary vertical tubes wider than the normal coenotube. Some of these, as in species of *Astrostylopsis* (Pl. 5, figs. 6, 7, 8), are associated with radial transverse tubes and are evidently axial astrotubes (Pl. 4, fig. 1). Even where not so associated, as in species of *Actinostromina*, the occasional presence of grouped axial offsets identifies such tubes as astrotubes (Pl. 4, fig. 7). In addition to such as these, there are often, in *Astrostylopsis* but not in *Actinostromina*, numerous others not so identifiable and with no relationships among themselves or with the reticulum to suggest that they are astrotubes (Pl. 5, figs. 1–3). Such tubes, it is true, might be autotubes (as in *Milleporidium* Steinmann and *Promillepora* Dehorne) or they might be lateral astrotubes (as in *Actostroma* Hudson): they have not, however, the clear-cut origin, individuality, and distribution of the former, or the pattern of distribution of the latter. In some cases they make up a large part of the reticulum; in other cases they are only sporadically scattered through it. The walls which enclose them are as fenestrate as other vertical lamellae and the microstructure is the same. They are, in effect, normal coenotubes which have developed vertically and become consistently tubular.

Laminae. When tabulae are vertically continuous within a considerable part of the reticulum they form an unbroken transverse platform which, in the study of Mesozoic stromatoporoids, is called a *lamina*. This is formed of tabulate tissue only, is not fibrous, and is formed subsequent to the pillars and vertical lamellae which thus pass through it. It should not be confused with the transverse lamellae which consist of either orthogonal or clinogonal fibrous trabeculae. It is not the laminae of the Palaeozoic stromatoporoids.

Astrosystem. The term astrorhizae was first used for the unwalled, branching, radiating grooves or gutters on the coenosteal surface of a stromatoporoid. It is now often used not only as a general term covering both these structures and those associated with them, whether on the surface of the coenosteum or within it, but also as a term for structures homologous with the astrorhizae and their associates even when the former are not present. Since the term has not only a specific meaning but also a functional one, it is not suitable for such general use. The term *astrosystem* is here used for such a group of

associated structures or for single structures homologous with them. Particular structures within the astrosystem are linked to it by use of the prefix *astro-* resulting in such terms as *astrotube*, *astrotabulae*, and *astrocorridor*.

Transverse astrotubes and offsets. The astrosystems of the Actinostromariidae consist of axial astrotubes with a number of transverse astrotubes radiating at vertical intervals and at right angles from them. These transverse tubes occur between adjacent transverse lamellae and since they are thus in general conformity with the rectangular pattern of the reticulum they are hardly distinguishable in vertical section from the transverse coenospaces except on polished surfaces (Pfender 1937, pl. 1, fig. 3). As far as is known such transverse tubes never ramify in the reticulum otherwise than horizontally or approximately so, nor do they develop vertically and become astrocorridors. In some of the species described these transverse tubes are so short that they are merely offsets from the vertical tubes.

SYSTEMATIC PALAEONTOLOGY

The superfamily Milleporellicae Hudson 1959 is characterized by clinogonal fibrous tissue. Forms belonging to the Actinostromariidae Hudson 1955 and the Siphostromidae Steiner 1932 have orthogonal or heterogonal fibrous tissue and are part of a group which has a well-defined identity in the Mesozoic Stromatoporoidea. It is here given systematic rank as a superfamily, the Actinostromariicae.

Though Germovšek rightly emphasized the marked variation in his six species mentioned earlier, it was not necessary to allocate them to five genera or to place them in different families. It is here shown that in all his species the microstructure of the skeletal tissue is orthogonal fibrous and the vertical pattern of the reticulum is, basically, regularly rectangular. They should therefore be all included in the Actinostromariidae.

[The family Trupetostromidae was founded by Germovšek (1954, p. 368) to include *Trupetostroma* Parks and his own two genera *Astrostylopsis* and *Trupetostromaria*. Its nominate genus *Trupetostroma* Parks 1936 is a Devonian genus of which the type species *T. warreni* Parks 1936 has only superficial resemblance to Germovšek's genera. The value and validity of this family can therefore be left to students of Palaeozoic stromatoporoids: it does not concern us.]

Generic allocation of Germovšek's species is difficult since the material on which they were founded is sparse and must not be completely sectioned. His species differ, in general, from described forms in the Actinostromariidae by the occurrence of cellular sclerenchyme, by the marked development of tubular reticulum, and by astrosystems of axial astrotubes usually with no, or limited, transverse tubes. These features are an expression towards structural verticality of the coenosteum, a trend which also occurs in the Milleporellicae and in other groups in the Actinostromariicae. In the former, vertical pillars or lamellae tend to be the sole structural element of the reticulum (as in *Milleporella* Deninger or *Stromatoporellina* Kühn): in both superfamilies there is a tendency for complex astrosystems with their important lateral elements to be replaced by isolated vertical astrotubes (as in *Actostroma* Hudson) and for the reticulum to include autotubes (as in *Milleporidium* Steinmann and *Promillepora* Dehorne). Germovšek's species can

be linked with species of *Actinostromaria* in a morphological series (not at present a phylogenetic one) illustrating such a structural change. There is thus justification for their inclusion in the Actinostromariidae.

Actinostroma Nicholson 1886, to which Germovšek allocated his species *grossum*, is a Silurian to Devonian genus with the holotype of its type species from the Middle Devonian of Gerolstein, Germany. The genus is characterized by non-fibrous skeletal tissue. Germovšek's species cannot therefore belong to it.

Actinostromaria Haug 1909, to which Germovšek's species *tubulata* was allocated, is defined below. A characteristic feature of *tubulata* is a marked tubular reticulum, a character which excludes it from *Actinostromaria*.

The three genera founded and named by Germovšek are *Actinostromina*, *Astrostylopsis*, and *Trupetostromaria*. The last two names, in my opinion, are synonyms, naming the same genus. For the following reasons, I here chose *Astrostylopsis* as the valid name for that genus and declare *Trupetostromaria* a junior subjective synonym of it. This latter genus was founded by Germovšek for the species *circoporea*, one of its diagnostic characters being the occurrence of vertically aligned cellular sclerenchyme, considered by Germovšek to form structures comparable to the 'porous pillars' of *Trupetostroma*. The comparison with *Trupetostroma* is superficial and since the name *Trupetostromaria* might be held to imply a relationship or similarity which does not exist, it is not preferred as the name of the genus in question.

When founding the genus *Actinostromina*, Germovšek considered the sole diagnostic feature to be a homogeneous granular microstructure which he stated was the only structural component of the trabeculae in the type species, *Actinostromina oppidana*. It is true that in the holotype, the greater part of any trabecula consists of an evenly mottled dark-coloured fine calcite. There is, however, in places, very fine crystal fibrous tissue orthogonally radial to it (Pl. 6, fig. 8). The dark-coloured calcite is, therefore, the calcification band and *Actinostromina* does not basically differ in trabecular structure from *Astrostylopsis* or from other genera of the Actinostromariicae. The species of the genus have, however, a coenosteal structure which differs from that of those genera and maintains *Actinostromina* as a functional genus.

Generic diagnostic morphology

Actinostromina. The reticulum of *A. oppidana* does not differ significantly from that of *Actinostromaria*. The abundant well-developed vertical tubes are considered to be astrotubes and therefore *Actinostromina*, like *Actinostromaria*, is characterized by astrosystems. Its astrotubes have, however, no associated transverse tubes, as are common in *Actinostromaria*, but only offsets which tend to be vertically developed. This distinction is of phylogenetic importance and *Actinostromina* Germovšek is therefore retained as an active genus. Germovšek recognized that *Actinostromina oppidana* and *Actinostroma grossum* were, structurally, basically similar and, but for the difference in microstructure, now shown to be non-existent, would be cogeneric, a conclusion with which the author agrees.

Actinostroma grossum grossum and *Actinostroma grossum robustissimum* were considered by Germovšek to be subspecifically distinct on the grounds that the reticulum mesh of the latter was slightly wider and its coenosteum was ellipsoid whereas that of *A. grossum grossum* was subsphaerical. These differences are so slight, if they do exist,

that they are within the range of individual variation: the subspecies are therefore considered synonomous.

Astrostylopsis. The two species, *A. slovenica* and *A. grabenensis*, for which this genus was founded are characterized by a partly tubular reticulum with some cellular sclerenchyme. The vertical tubes are considered to be coenotubes, and the reticulum to be transitory to an entirely tubular reticulum such as that of *Siphostroma* Steiner. This structure does not occur in any known genus of Actinostromariidae and *Astrostylopsis* Germovšek is therefore considered to be an active genus.

References were made to Germovšek's genus *Astrostylopsis* by Hudson (1957, 1958). In the first of these papers the genus was considered to be a synonym of *Stromatorhiza* Bakalow 1906, a conclusion now known to be ill founded since its skeletal issue is orthogonal fibrous whereas that of *Stromatorhiza* is generally granular. In the 1958 paper *Astrostylopsis* and *Trupetostromaria* were compared with *Actostroma* Hudson 1958 and considered to be generically distinct.

Actinostromaria darroensis was described from the Upper Jurassic of southern Ethiopia by Zuffardi-Comerci (1932, p. 74, pl. 2, fig. 7) and by Wells (1943, p. 49, pl. 8, figs. 6–8) from eastern Ethiopia. The species has a tubular polygonal reticulum with scattered axial astrotubes with small irregularly developed transverse tubes. The species should be placed in the genus *Astrostylopsis*.

Trupetostromaria. This genus was founded for the species *circoporea* which differs from the species of *Astrostylopsis* only by the much wider mesh of its more tubular reticulum and by the much more abundant cellular sclerenchyme, that is, it has the characteristic features of *Astrostylopsis* better developed. There are no structures in *Trupetostromaria* not present in *Astrostylopsis*: the two genera are therefore synonymous.

Superfamily ACTINOSTROMARIICAE nov.

Stromatoporoidea with radial or bilateral orthogonal or heterogonal fibrous trabeculae.

Family ACTINOSTROMARIIDAE Hudson 1955

Actinostromariicae with reticulum of vertical pillars and/or pillar-lamellae, and transverse bars or widely meshed transverse lamellae. Vertical reticulum variously rectangular; transverse reticulum labyrinthic or tubular. Cellular sclerenchyme variously developed or absent. Astrosystems of axial astrotubes with or without variously developed and variously radial transverse astrotubes or offsets. Trabeculae orthogonal fibrous.

Genus ACTINOSTROMARIA Haug 1909

Type species (by monotypy) *Actinostromaria stellata* Haug 1909.

Diagnosis. Actinostromariidae with vertical reticulum regularly but discontinuously rectangular with vertical pillars better developed and slightly coarser than the transverse bars. Transverse reticulum puntal or with angular labyrinthic or polygonal mesh. Axial astrotube(s) about same width as coenospaces, with, at regular vertical intervals, well-developed branching transverse astrotubes.

Genus ACTINOSTROMINA Germovšek 1954

Type species (by monotypy) *Actinostromina oppidana* Germovšek 1954.

Diagnosis. Actinostromariidae with reticulum of discontinuous vertical pillars and connecting lamellae, and a very open transverse lamellar net, both about equally developed; sparse cellular sclerenchyme. Vertically the reticulum is irregularly and discontinuously rectangular; transversely it is a loose irregular mesh of open (rarely closed) labyrinthic coenospaces. Astrosystems of well-developed, sparsely tabulate; walled, solitary astrotubes with or without offsets or, more rarely, indefinite irregular transverse tubes, both vertically disposed. No coenotabulae.

EXPLANATION OF PLATES 4 AND 5

All figures are of thin sections of the holotypes of various species of Germovšek. The dark line in all figures is the calcification band in the mid-plane of the trabeculae: the light grey on either side of it is the fibrous tissue, the clear white being where this has been removed during preparation of the section. The fibrous tissue often completely fills the coenospace or coenotube. Some of the coenotubes and astrotubes, filled with dark mud, have been cleared in the photos.

PLATE 4

Figs. 1, 2, 8. *Astrostylopsis circoporea* (Germ.). 1, Trans. sect. P14*d*, ×8. Note radial transverse tubes separated by cellular sclerenchyme. 2, Vert. sect. P14*b*, ×8. Grouped tubes are probably through astrosystem though not through axial astrotubes. 8, Vert. sect. P14*a*, ×6·7, as Germovšek, pl. 8, fig. 1*a*.

Fig. 3. *Actinostromina oppidana* Germ. Trans. sect. P5*b*, ×8. No vertical section available.

Fig. 4. *Actinostromina grossa* (Germ.). Vert. sect. P1*a*, ×6·7, as Germovšek, pl. 1, fig. 1*a*. Right side crushed. Note astrosystem and cellular sclerenchyme lower left.

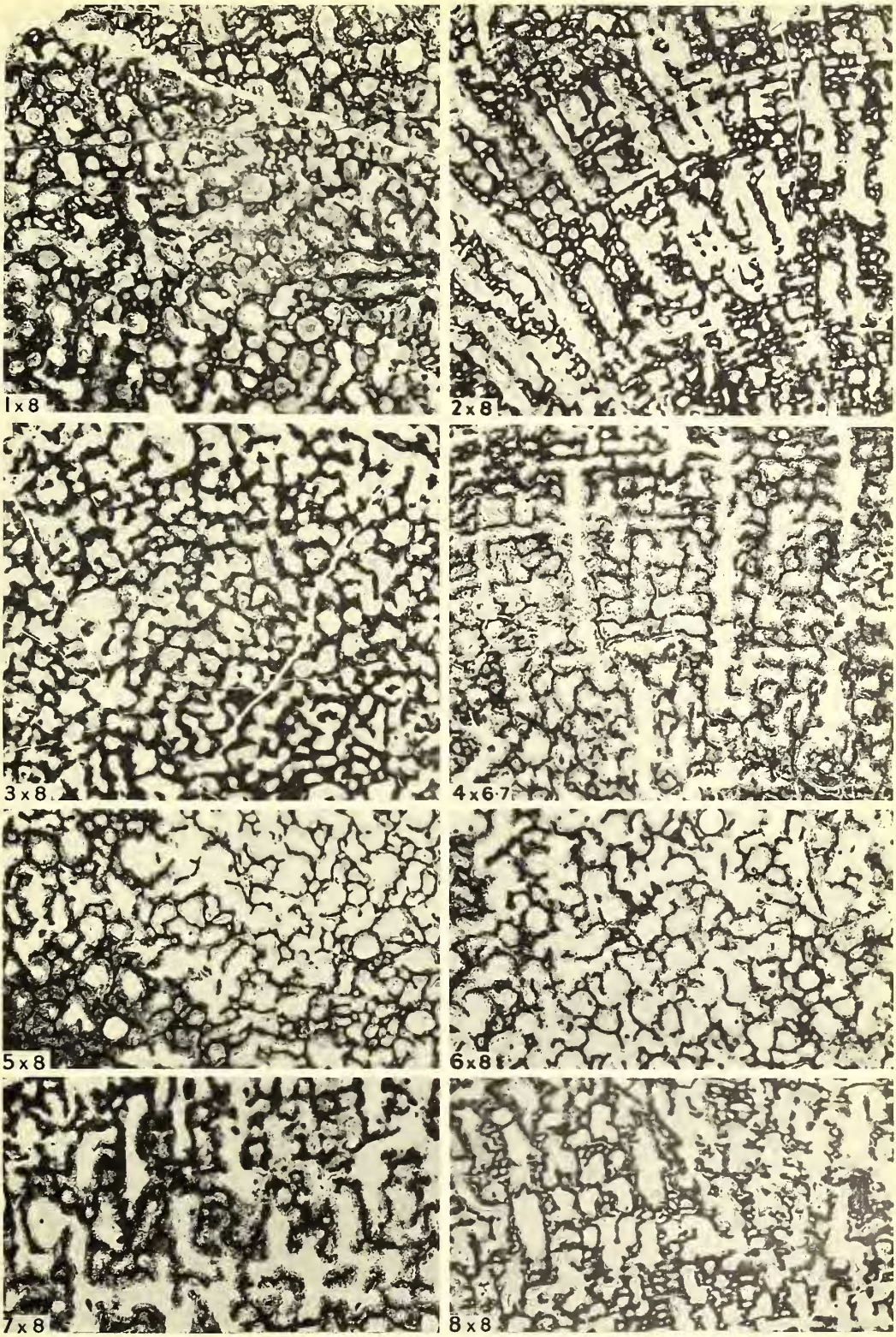
Figs. 5, 6, 7. *Actinostromina grossa* (Germ.), from holotype of *Actinostroma grossum robustissimum* Germ. 5, Trans. sect. P2*a*, ×12. Reticulum mesh partly destroyed. 6, Trans. sect. P2*b*, ×8. Note widely cellular sclerenchyme. 7, Vert. sect. P2*b* (same section as fig. 6), ×8. Section through astrosystems.

PLATE 5

Figs. 1–3. *Astrostylopsis tubulata* (Germ.). 1, Vert. sect. P3*b*, ×6. Note fenestrate vertical lamellae, axial and transverse astrotubes on upper left, vertical tubes on upper right probably through astrosystem though not through axis. 2, Trans. sect. P3*d*, ×8. Note coarse cellular sclerenchyme. 3, Vert. sect. P3*a*, ×6·7, same sect. as Germovšek, pl. 1, fig. 2. Note coenotubes separated by cellular sclerenchyme.

Figs. 4–6. *Astrostylopsis slovenica* Germ. 4, Trans. sect. P12*c*, ×8. Note cellular sclerenchyme bounding transverse astrotubes. 5, Vert. sect. P12*e*, ×8. Note narrow transverse tubes radial to axial astrotube. 6, Trans. sect. P12*d*, ×8. Note irregular transverse astrotubes.

Figs. 7, 8. *Astrostylopsis grabenensis* Germ. 7, Trans. sect. P13*b*, ×8. Note coarse cellular sclerenchyme in astrosystems. 8, Vert. sect. P13*a*, ×6·7, as Germovšek, pl. 7, fig. 2. Lower part crushed. Note fenestrate lamellae in upper part.



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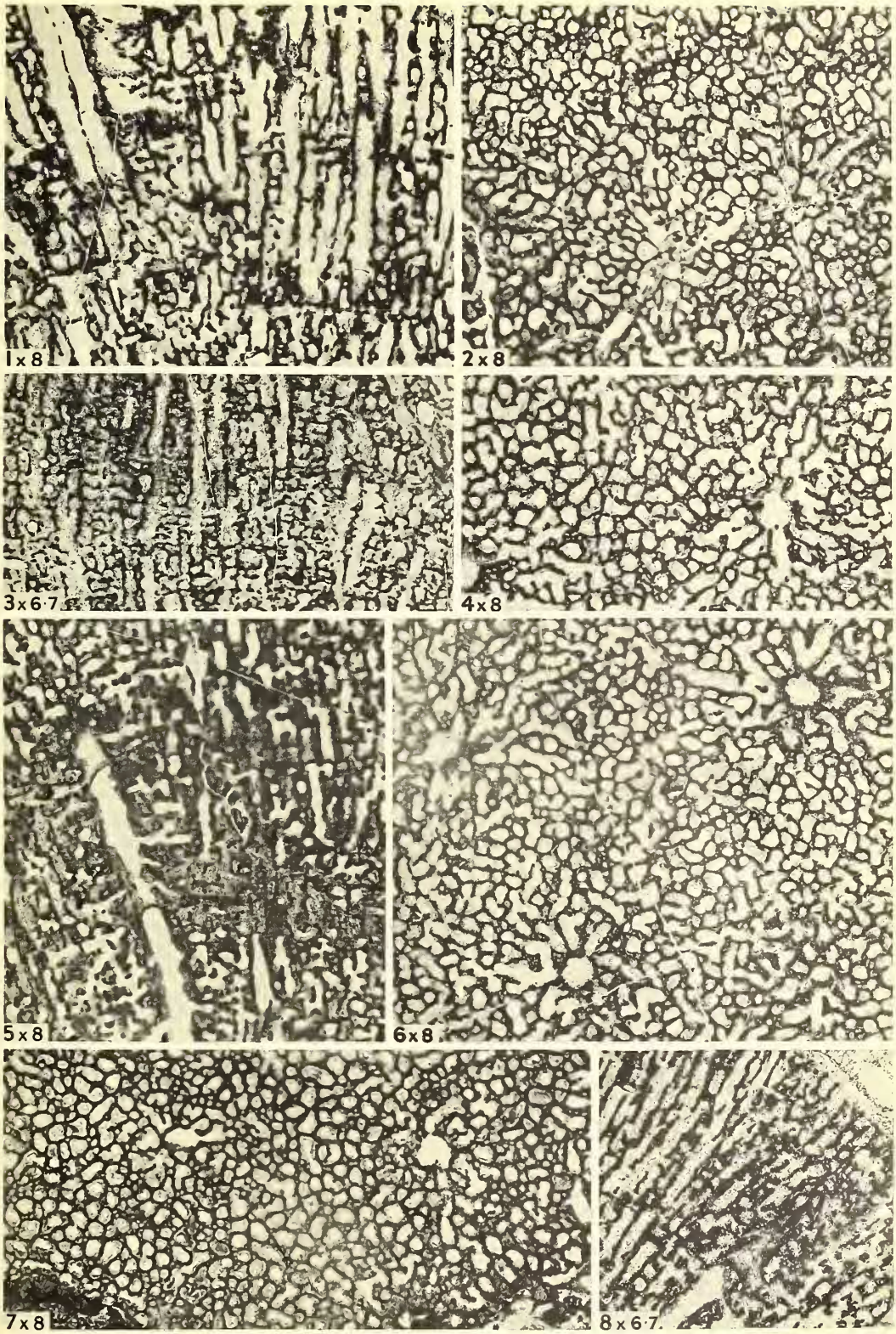

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